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BEHAVIOR AND ECOLOGY OF THE ENIGMATIC ANT
LEPTANILLA JAPONICA BARONI URBANI
(HYMENOPTERA : FORMICIDAE : LEPTANILLINAE)

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SUMMARY

The present study of *Leptanilla japonica* has clarified for the first time the biology of the Leptanillinae. Males were obtained, which are the first specimens of the subfamily to be collected in association with workers. *L. japonica* is a totally subterranean ant. Colonies are monogynous with a dichthadiiform queen. Worker population per colony is small, usually 100-200. Development of immature individuals is strictly seasonally synchronized. Colonies often emigrate to the site of paralyzed prey (geophilomorph centipedes). For carrying larvae workers grasp peculiar structures projecting from the larval prothorax with the lower mouthparts. The final-instar larvae have a pair of specialized lateral duct organs on the 4th abdominal segment. Through these organs larval hemolymph is provided for consumption by adults, especially by the queen. Nutrition of the queen depends exclusively on this process. The frequency of larval hemolymph feeding by queens is abruptly elevated when the larvae mature. Owing to this the queen is able quickly to achieve full physogastry, and to lay a batch of 100-200 eggs within a few days. Emergence of new workers from pupae is synchronized with hatching of the 1st-instar larvae from the eggs. In a concluding section the lifemode of *Leptanilla* is compared with that of doryline and ecitonine army ants.

RESUME

Comportement et écologie de la Fourmi énigmatique
Leptanilla japonica Baroni Urbani
(Hymenoptera : Formicidae : Leptanillinae)

Le présent travail sur *Leptanilla japonica* donne pour la première fois des informations sur la biologie des Leptanillinae. Deux mâles ont été obtenus, qui sont les premiers spécimens à être recueillis en même temps que les ouvrières de la même espèce, chez les Leptanillinae. *L. japonica* est une fourmi entièrement souterraine. Ses sociétés sont monogynes, avec une reine dichthadiiforme. Le nombre d'ouvrières d'une société est faible : en général 100 à 200. La croissance du couvain est strictement synchronisée avec

la saison. Les sociétés se déplacent souvent jusqu'à l'endroit où se trouve la proie paralysée (Chilopode géophilomorphe). Les ouvrières, pour porter les larves, saisissent avec leurs pièces buccales inférieures (labium et maxilles) la structure particulière qui fait saillie ventralement sur le prothorax larvaire. Les larves du dernier stade ont une paire d'organe canaliculaires latéraux sur le quatrième segment abdominal. Par cet organe l'hémolymphe larvaire est excrétée, pour l'alimentation des adultes, et particulièrement de la reine. La nutrition de la reine dépend exclusivement de ce processus. Quand les larves sont proches de la nymphose, la fréquence de cette activité alimentaire (appelé "LHF") augmente de manière brusque, permettant à la reine de devenir rapidement physogastre, et de fournir 100 à 200 œufs en quelques jours. L'éclosion de larves du premier stade est synchronisée avec l'émergence de nouvelles ouvrières. En conclusion, le mode de vie de *Leptanilla* est comparé à celui de Fourmis nomades, Dorylinae et Ecitoninae.

INTRODUCTION

The Leptanillinae is a small ant subfamily containing about 30 named species of which 16 were described from males unassociated with conspecific workers (BARONI URBANI, 1977). It has been assumed from the adult morphology, especially dichthadiiform of the queens, that the leptanillines have legionary habits like those of the tropical army ants of the subfamily Dorylinae (*sens. lat.*) (WILSON, 1971). Nothing, until now, has been known of their life history. Leptanillines were initially placed as a tribe of the former subfamily Dorylinae (EMERY, 1910), but were later raised to subfamily rank (WHEELER, 1923, p. 335). This change was based mainly on several aberrant features of larval morphology (WHEELER and WHEELER, 1930). According to WHEELER and WHEELER (1965) the most notable of these are (1) the peculiar projection from the ventral surface of the prothorax; (2) the reduction of the spiracles from the usual ten pairs to a single pair located on the 3rd abdominal segment; and (3) the shape and stance of the outwardly-directed mandibles. All of these are unique to leptanillines among the Formicidae, but their functions have been totally unknown.

Five species of *Leptanilla* have been described from Japan (BARONI URBANI, 1977), but the collection of suitable material, even in that country, has been too incidental to allow detailed studies on their biology. Recently, however, I have collected eleven colonies of *Leptanilla japonica* BARONI URBANI from Cape Manazuru in southern Honshu. This material has permitted informative studies on the ecology and behavior of *Leptanilla*. The results of my field and laboratory observations are presented here, with discussion on the peculiar mode of life of *L. japonica*, which is apparently related to its presumed highly migratory habits.

MATERIALS AND METHODS

Leptanilla japonica is a tiny, yellow ant; the worker is about 1.2 mm long and the queen 1.8 mm long. Between July 1981 and August 1983 eleven colonies of this species were collected in the evergreen broadleaf forest at Cape Manazuru, Kanagawa Prefecture. All colonies were unexpectedly located in soil during excavation in search of other subterranean ants. Because the volumes of the nest chambers were so small colonies were easily collected in their entirety. Since the brood is rather delicate the ants were not aspirated into a vial; instead, small lumps of soil surrounding each whole colony were carefully put into a vial *in toto* and brought back to the laboratory. Of the 11 colonies collected six were cultured (at 20-25° C). Colonies were kept in rectangular clear polystyrene containers (10 × 11 × 2 cm) with a floor-cover of gypsum mixed with activated carbon powder; no brood chamber was provided. Activities were monitored through clear glass covering the tops of the containers, with the aid of a swing-arm-stercomicroscope (magnifications 10-80X). Sufficient prey was given to prevent starvation, and small geophilomorph centipedes alone were accepted by the ants (see below). The observed behavioral acts were noted using a sound recorder, or logged directly onto a portable microcomputer (Epson HC-20), for assaying time budgets. Scanning electron micrographs were taken with a J.E.O.L. JSM-25 microscope after material had been critical-point-dried with liquid CO₂ or treated with hexamethyldisilazane (NATION, 1983).

RESULTS

Nesting habits and colony composition

1. *Nesting habits*

All the nests were situated at a depth of 10-15 cm in moist well-packed earth. Ten colonies were found in the soil without covering material except leaf litter, and one was found in the soil under a large fallen dead branch.

In most cases the whole colony occupied a single, narrow, irregular space, which apparently was not excavated by the ants themselves but was a preformed crevice. In some cases, perhaps influenced by the form and distribution of the crevices, the ants were located in a few adjacent but separate chambers. The brood, if any, was cramped into a single pile without separation of eggs, larvae or pupae. When disturbed by excavation the queen and workers, whether they were alone or carrying larvae, disappeared swiftly into small cracks in the soil. This behavior is facilitated by their dorsoventrally flattened and freely movable body sections, which permit them to move easily in confined tortuous spaces in the soil. Underground tunnels were not noted at the peripheries of nest chamber.

2. Adult population

Table I shows the composition of the Cape Manazuru colonies. The collections are ordered so that they reflect the inferred seasonal cycle, regardless of individual times of collection. Queens were collected with 10 of the 11 colonies and all were monogynous. Worker population per colony is estimated to range from 100 to 200. Among the completely collected samples in the active season, however, some colonies (82-130, 82-222 and 82-314) contained many fewer workers relative to the numbers of larvae or pupae present. In these it is inferred that a large portion of workers were probably out foraging, or had expired.

3. Seasonal trend of immature development

From *table I* it can be seen that broods were produced in discrete generations. Furthermore, in each generation all individuals were at approximately the same stage of development in each colony, i.e., all larvae were of the same instar and size, or pupae were similarly pigmented. From the seasonal trend seen in *table I*, and the results of laboratory rearing (see below), the average worker-brood cycle of *L. japonica* is surmised as follows (*fig. 1*):

In a short period of July (late mid-summer) a batch of eggs is laid by the queen; these hatch into larvae, at the latest by early August, and subsequently develop in concert until winter, when they hibernate, to complete development the following summer. Most larvae appear to reach the final instar before hibernation. This is suggested by the fact that there were no significant differences in head length and other morphological features examined with the SEM in comparing larvae from winter colonies (82-33 and 83-40) with those taken in summer (82-222 and 82-314). In the following July the larvae all pupate synchronously, and the queen then promptly lays the next batch of eggs. (The larvae of *L. japonica* do not spin cocoons prior to pupation). New adults emerge from pupae between late July and early August. The synchronization between larval hatching and adult eclosion was confirmed in the laboratory: In colony 81-173, which was collected on 11 July 1981 with about 100 eggs and 140 worker pupae, new workers emerged from most of the pupae on 26 and 27 July, while the 1st-instar larvae hatched from most of the eggs around 23 July. This result suggests that the composition of colonies 82-217 and 82-219 at collection probably indicates that hatching of larvae in nature slightly precedes eclosion of new adult workers (see *table I*).

As is the case with the larvae of most ant species, there is no information on the number of larval instars in *L. japonica*. However, their hatching in July and attainment of the final instar by mid November, at latest, in the same year, suggest rapid larval growth in this species. (Most subterranean ant species at Manazuru forest cease their extranidal activities in mid November when the soil temperature at 15 cm deep falls below 15° C; MASUKO, unpubl.). In all colonies where pupae were found a small number of individuals remained as larvae (5-10 % of total, see *table I*). These larvae seemed from their size to be of the same generation as the pupae.

Table I. — Field data on 11 colonies of *Leptanilla japonica*.
 Tableau I. — Données recueillies sur le terrain pour la population de 11 sociétés de *L. japonica*.

Colony no.	Date of collection	Queen	Workers	Male	Eggs	Hatchlings	Final-instar larvae	Pupae	
								worker	male
83-14	16.i.83	1	135	0	0	0	138	0	0
83-40	20.ii.83	0	25	0	0	0	31	0	0
82-33	7.iii.82	1	127	0	0	0	86	0	0
82-130	19.v.82	1	29	0	0	0	c. 200	0	0
81-173	11.vii.81	1 ^a	100	0	c. 100	0	9	136	1 ^b
82-217	14.vii.82	1	c. 80	0	0	c. 150	10	c. 200	0
82-219	14.vii.82	1	c. 70	1	—	c. 50	15	c. 200	0
82-222	14.vii.82	1	31	0	c. 130	—	18	220	0
83-97	3.viii.83	1	49	0	9	4	6	116	0
83-105	3.viii.83	1	42	0	1	1	4	81	0
82-314	17.viii.82	1	15	0	0	0	198	0	0

^a When collected in the field, only this queen was slightly physogastric while the others were not at all.

^b This male pupa emerged as an adult later in the laboratory.

^c Au moment de la récolte dans la nature, seule cette reine était légèrement physogastric ; les autres pas du tout.

^d Cette nymphe a fourni un mâle adulte, au laboratoire, un peu plus tard.

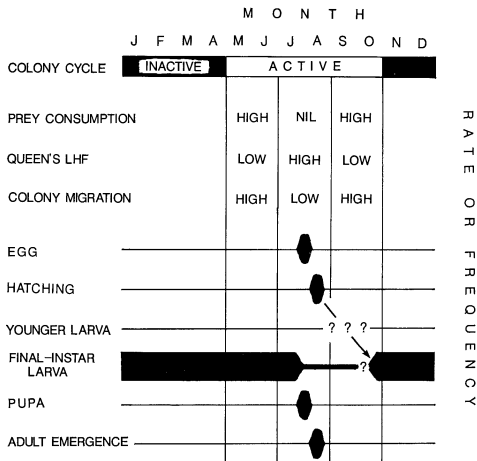


Fig. 1. — Seasonal cycle of colony functions of *Leptanilla japonica*. For explanation see text.

Fig. 1. — Cycle saisonnier des différentes fonctions sociales de *L. japonica*. Pour les explications, voir le texte.

4. Production of sexuals

The characteristics of sexual production of *L. japonica* remain poorly known, since the material obtained in this study is scanty. A male-pupa and an adult male were collected in the field with colonies 81-173 and 82-219, respectively (table 1). These are the first male specimens in the Leptanillinae to

have been collected from a colony, and confidently associated with workers. They will be described elsewhere (OGATA, TERAYAMA and MASUKO, in prep.). Absence of gyne-pupae, and the extremely small number of males, suggest that they were produced irregularly in this case. At the time of collection the worker-pupae of colony 81-173 were not at all pigmented; the male-pupa had, however, already darkened to some extent. A male ultimately emerged earlier than workers in the laboratory. The male of colony 82-219 had already emerged in the field at a time when worker-brood was still at the pupal stage.

Laboratory observations

Six colonies were observed in the laboratory for varying periods. Four of them (colonies 81-173, 82-217, 82-219 and 82-222) which included pupae when collected perished within 1-3 weeks of the beginning of culture, because of fungus infection. The other 2 colonies (82-33 and 83-14) were both collected with larvae, in winter. Their longer period of survival (43 days for colony 82-33 and 103 days for colony 83-14) permitted the study of details of larval development up to pupation, and of activities of the queens and workers. Descriptions in this section are based chiefly on observations on these colonies. When larvae of colonies 82-33 and 83-14 attained their full growth, with swollen bodies, the queen abruptly entered physogastry and prey consumption by the colony was terminated. To facilitate discussion the colony stage before this change is referred to below as the "larval-growing stage" and the stage thereafter the "egg-laying stage". Similar, if not homologous, changes in colony behavior are well known between the alternating "nomadic" and "statory phases" of some tropical army ants (SCHNEIRLA, 1971). The temporal use of nest sites in the field (discussed above), the convergence to army ants in adult (especially queen) morphology, and the frequent colony migrations observed in the laboratory (see below) suggest strongly that *L. japonica* is a highly migratory ant. The terminology used to describe the behavioral cycles of army ants has not been followed here, however, in the absence of direct field evidence of colony migration correlated with changes in the brood composition of colonies of this species.

Activities of workers and development of larvae

1. Brood pile and guard ants

When laboratory rearing began the number of living larvae had reduced to only 12 in colony 82-33 and to about 100 in colony 83-14, because of injuries sustained in collection and transportation. The transfer of the ants to laboratory nests at first greatly disturbed them, and resulted in their being scattered over the plaster floor for a short time. By the next day, however, they were normally aggregated and all the larvae had been gathered into a

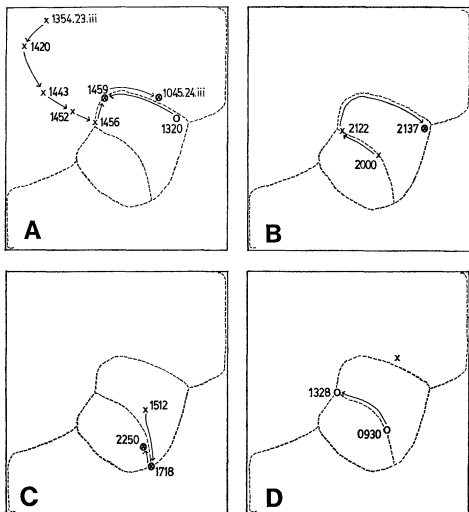


Fig. 2. — Diagrams of a trail system of *Leptanilla japonica*, observed in a laboratory colony. The courses of trails (broken line) were persistent during the culture. The outer rectangles represent the confines of an artificial nest (10×11 cm). Trajectories of prey transport and colony migration are shown for three cases of predation (A-C) and one case of colony movement without prey consumption (D). X = site of retrieved prey; O = colony site where the queen and brood existed; \bar{x} = site of prey feeding by colony. Of a series of x's in each figure, the first one represents the position where the prey was first recognized as completely immobilized. Each symbol is accompanied with hour of day when the locations were recorded. A: March 23-24, 1982. B: March 26, 1982. The colony remained at the same place, while the prey was moved from the site of its complete paralysis at 2000. C: March 29, 1982. The prey completely immobilized at 1512 reached the colony site at 1718; then the ants, together with the prey, moved along a trail to the

single pile. This was flat, loosely organized, and attended by some dozens of workers, while others engaged in foraging activity. Interestingly, the queens spent most of their time on the brood pile. Half, or more, of the workers at the pile stood at its periphery. They were apparently guard ants, since most of them faced outward and took a characteristic posture, with the anterior half of the body raised, the forelegs suspended in the air, and the mandibles open. They frequently rushed to approaching objects such as nestmates. Such guards also gathered around the spot where larvae were feeding on retrieved prey. Other workers present at the brood pile engaged mostly in larval care or nestmate-grooming.

2. Trail system

Throughout the period of laboratory life a conspicuous trail system, on which the ants travelled, was observed on the floor of the nest chamber (fig. 2). The course of the pathways often changed with time. Even when undisturbed the movements of workers along the trails were not organized: each worker came and went from the brood pile area independently, so that there was no apparently organized movement in groups. Some workers departed from the trails to stray singly, and apparently randomly, over the interior of the containers.

When the queens and unladen workers moved on the trails their abdomens were lowered, apparently causing the ventral surface to touch the substrate. In the case of workers it appeared that the sting was not protruded on the trails at this time. This suggests that a sternal gland secretion partici-

place recorded at 2250. D: April 2, 1982. Colony migration occurred between 930 and 1328 on April 2 and the ants remained at the place recorded at 1328 until 20 April when their rearing was terminated. The prey given at 2251 on 3 April was found paralyzed at x at 2358 on the same day but it remained intact until 20 April.

Fig. 2. — Diagramme du système de pistes de *L. japonica*, observé au laboratoire (société 82-33). Les pistes (lignes tiretées) ont persisté durant l'élevage. Le contour rectangulaire extérieur représente les limites du nid artificiel (10 × 11 cm). Les trajets suivis pour le transport de la proie et pour le déplacement de la société sont représentés pour 3 cas de chasse (A, B, C) et un cas (D) de déplacement de la société sans qu'il y ait eu consommation de proie. X = position de la proie; O = position de la société; (x) = lieu de consommation de la proie par la société. Dans une série d'x, le premier indique l'endroit où la proie a été immobilisée. L'heure est indiquée à côté de chaque symbole. A: 23-24 mars 1982. B: 26 mars 1982. La société ne s'est pas déplacée, tandis que la proie, paralysée à 20 h., a été amenée jusqu'à la société. C: 29 mars 1982. Paralysée à 15 h. 12, la proie a atteint la société à 17 h. 18; ensuite les Fourmis, traînant la proie, se sont déplacées le long d'une piste, jusqu'à l'emplacement enregistré à 22 h. 50. D: 2 avril 1982. La société s'est déplacée entre 9 h. 30 et 13 h. 28, le 2 avril et elle est restée à l'endroit enregistré à 13 h. 28, jusqu'à la fin de l'élevage (20 avril). La proie, donnée à 22 h. 51, le 3 avril, a été trouvée à 23 h. 58 en x, paralysée; mais elle est restée là, intacte, jusqu'au 20 avril.

pates in formation of the trails, as in the case of *Onychomyrmex*, an Australian army ant genus related to *Amblyopone* (HÖLLDOBLER and TAYLOR, 1982). The results of histological investigations on the exocrine glands of *L. japonica* will be published elsewhere (HÖLLDOBLER, PALMER, MASUKO and BROWN, in press).

3. Prey capture

No field data was obtained on the feeding habits of *L. japonica*. Instead, different soil invertebrates were given to laboratory colonies to test food preferences in the larval-growing stage (as defined above).

Although organisms such as an annelid (ca. 5 mm long), a nematode (ca. 5 mm long), a campodeid (ca. 3 mm long), *Isotoma collembolans* (ca. 1.5 mm long), and ant larvae (*Oligomyrmex sauteri* Forel) were totally ignored (tested once for each), geophilomorph centipedes of small size (body length ranging 10-20 mm) were invariably stung, paralyzed and ultimately consumed. The centipedes were given to the ants either in an intact condition or, if active enough to disturb the culture, in an injured state. During 22 days of its larval-growing stage colony 82-33 hunted and consumed 7 intact geophilomorphs (10-15 mm long; mainly nymphs of *Prolamnonyx holstii* (Pocock)), and fed partly on a cryptopid (13 mm long), but rejected the chopped body (5 mm long) of a *Strigamia* species and a segmented piece (15 mm long) of an undetermined larger geophilomorph. During its 52-day larval-growing stage colony 83-14 consumed 14 intact or injured geophilomorphs (12-20 mm long; mainly *Prolamnonyx holstii* nymphs), 3 pieces of chopped portions (each 5 mm long) of unidentified larger species, and a cryptopid (15 mm long).

Such predation on small geophilomorphs, and the characteristic mode of larval feeding on these organisms (see below), suggest that *L. japonica* preys chiefly or exclusively on these centipedes in nature. Recently, a single colony of an undescribed species of *Leptanilla* was collected on Formosa. Its larvae, when discovered, were found clustered on a captured geophilomorph (OGATA, TERAYAMA and MASUKO, in prep.).

Under laboratory observation workers which came upon centipedes instantly attacked them. The ants tenaciously seized and stung the prey until it was completely paralyzed (fig. 3). In most cases the centipedes were immobilized within 10 minutes of their introduction and attack by only several workers was sufficient to accomplish this paralysis, which is expressed as an inhibition of motor activity. I observed once, during the egg-laying stage of colony 82-33, that a geophilomorph (15 mm long) which had been paralyzed but was thereafter ignored by the ants, remained alive, moving its appendages for 17 days, until it was preserved for study (see fig. 2D).

4. Larval and prey transport

Soon after a centipede is paralyzed nearby workers begin to drag it towards the brood pile. There is often a concurrent migration of the whole

egg deposition by pulling eggs from the queen's cloaca with their mandibles. A total of about 20 eggs were found in the larval pile. Eggs were ellipsoidal with long axis 0.26 ± 0.01 mm and short axis 0.18 ± 0.01 mm (mean \pm S.E.; $n = 10$; measured on preserved material at 160X).

On 17 March eggs numbered about 50 and most larvae had begun to purge their digestive tracts. Workers assisted them to discharge fecal masses and at times fed on the material so produced. On 19 March prepupae totaled about 40 and the number of eggs had reached about 100 (although about 20 % of them were collapsed, for an unknown reason, and workers were seen attaching their mouthparts to some of the eggs). Around this time the number of ants at the brood pile clearly increased, despite reduction in the total worker population (in which 50-60 workers now survived). This indicates that, in the egg-laying stage, most of the colony worker force is involved in brood care, while foraging is inactivated.

Oviposition by the queen lasted for a week after 16 March, and was not observed on 24 March when her gaster was still slightly distended, with a diameter of about 0.50 mm. By then the number of eggs had reduced to about 30. On 27 March there were about 30 prepupae and 30 worker-pupae, but all eggs had disappeared without producing hatchlings. There remained also 9 larvae, one of which had a swollen thorax. On 29 March the queen's gaster had completely contracted to its initial state, and by 30 March nearly all the prepupae had pupated. Workers were observed to help them shed the last larval skin. Most pupae had become pale-yellow on 18 April. Four geophilomorph centipedes and one cryptopid were paralyzed but then ignored by the ants between 9 March and 18 April, during the period of queen physogastry.

From 20 April the ants began again to consume newly introduced and captured centipedes. On 27 April all pupae had been destroyed by mites, so that laboratory rearing was terminated and the surviving members (the queen, 27 workers, and 5 larvae) were fixed for other studies.

Activities of newly emerged workers are precocious, since, in colony 81-173 where about 70 new workers successfully eclosed, such unpigmented workers, only one or two days after emergence, were observed to travel along the trails in the same manner as old workers.

The relationships between larval growth, egg production, predatory activity and colony migration in *L. japonica* colonies may be summarized as follows (see also *fig. 1*). In the larval-growing stage intensive predation on geophilomorph centipedes occurs repeatedly; the larvae consume this prey and grow in synchrony, while the queen remains with a contracted abdomen. Colony migration is frequent, in response to prey acquisition. When the larvae mature colonies enter the egg-laying stage. The larvae pupate synchronously; prey is no longer hunted; and the queen swiftly accomplishes physogastry, to lay a batch of eggs. Colonies at this stage become stationary,

constructed on the queens of both colonies 82-33 and 83-14. On the basis of the preliminary data on queens 82-33 more systematic observations were made on queen 83-14, whose data are summarized in *table III* and discussed below.

1. Rest

In the larval-growing stage the contracted queens spent most time resting, usually standing motionless on the larval pile (*table III*). It is curious that queens at rest invariably keep their gasters raised obliquely, at angles ranging from about 20° to 70° (mostly 50° - 60°), from the horizontal (*fig. 7*, arrow). The function of this posture is not clear. Furthermore, small but obvious gastral pulsations occurred at regular intervals of 10-15 seconds. These movements might be linked to functioning of the aorta. The queens rarely descended from the brood pile, except when large numbers of larvae were placed on the prey, at which times the brood pile usually became diffuse. For defecation the queens regularly left brood pile to excrete a milky droplet (nearly as large as an egg), usually about 5 mm from the periphery of the pile. Such excreta remaining at the abdominal tip of a queen were observed once to attract several workers which attached their mouthparts to it in turn, and finally ingested it.

Disturbance by the observer caused queens to leave the pile and to travel along the foraging trails. Workers encountering such a queen were totally indifferent, and passed without response of the kind which would be expected during colony emergency in other ant species.

From this rather inactive condition the queens entered an almost "restless" state which developed over a period of only a few days; the time proportions of active and resting periods were thus completely reversed (*table III*), with the active periods being occupied by larval hemolymph feeding.

2. Larval hemolymph feeding (LHF)

The term "larval hemolymph feeding (LHF)" was first coined for the primitive ponerine ant *Amblyopone silvestrii*, to denote an aberrant form of feeding in which adult ants (generally queens) pierce the dorsal integument of the abdomen of older larvae by pinching with the mandibular tips, and then feed on hemolymph oozing from the single resulting puncture (MASUKO, 1986). Although LHF in *Leptanilla* is functionally very similar to that in *Amblyopone* there is an important difference. *Leptanilla* queens imbibe hemolymph from a pair of specialized duct organs placed bilaterally on the 4th larval abdominal segment, without damaging the integument (*figs. 10 and 11*; MASUKO, 1989). These organs were previously regarded as spiracles (WHEELER and WHEELER, 1965). My behavioral and histological studies have confirmed that they are duct organs tapping the larval body cavity to the

Table III. — Comparison of percentage time spent on each behavior by the queen of colony 83-14 of *Leptanilla japonica* between her contracted and physiogastric conditions. The behavior was recorded continuously for 90 minutes or more on each observation day. For each behavior, the means of percentage time during 22-24 January and 11-13 March were calculated and statistically analyzed for equality by two-tailed *t*-test after arcsine transformation. In spite of the small sample size ($n = 3$), the mean differences are significant for rest ($P < 0.05$), LHF ($P < 0.05$), and being licked by worker ($P < 0.01$).

Tableau III. — Pourcentage de temps consacré à chaque type de comportement par la reine de la société 83-14 de *L. japonica*. Comparaison entre les périodes où la reine a l'abdomen contracté, ou bien est physiogastrique. Le comportement a été enregistré de manière continue pendant 90 minutes ou plus, chaque jour d'observation. Pour chaque type de comportement, les moyennes des pourcentages de temps, du 22 au 24 janvier et du 11 au 13 mars, ont été calculées et soumises à l'analyse statistique par le test de Student, après transformation en arcsinus. Malgré la taille réduite de l'échantillon ($n = 3$), les différences entre les moyennes sont significatives pour repos ($P < 0.05$), LHF ($P < 0.05$), et léchage par des ouvrières ($P < 0.01$).

Condition of queen	Contracted						Fully physiogastric			<i>t</i> _s
	Date in 1983	22 Jan	23 Jan	24 Jan	11 Mar	12 Mar	13 Mar			
Behavioral acts										
Rest		75.1	69.5	51.6	38.1	38.2	21.3			3.53
LHF		7.1	10.8	13.0	28.2	20.7	18.2			3.62
Hold worker		0	1.3	0	0	0	0.3			ns
Self-groom		0.5	1.3	0.9	1.1	1.7	10.7			ns
Be licked by worker		5.0	1.1	9.7	19.0	27.6	22.9			4.91
Other activities										
on brood pile		11.6	14.9	21.7	13.5	11.7	24.7			ns
on substratum		0.6	1.1	2.9	0	0	2.0			ns
Total		99.9	100.0	99.9	99.9	99.9	100.1			
Sample time (min)		90	92	92	100	100	100			

ns: Not significant.

47 % in her physogastric and contracted conditions, respectively). The mean duration of a single bout of hemolymph feeding from the duct organs was not significantly different between the two conditions of gastral inflation—101 sec. when physogastric (S.D. = 66, $n = 17$) versus 116 sec. when contracted (S.D. = 85, $n = 7$) (one-way ANOVA, $F_{1,22} = 0.23$). Furthermore, workers facilitated the queen's LHF by placing larvae near her. Queens sometimes treated a nearby worker almost like a larva. They held its trunk with their legs, nipping along its length. The worker remained immobile with the body lowered during this manipulation, and was always released after a few seconds.

3. Grooming

The queen in physogastry received significantly more frequent grooming by workers than when in a contracted condition (table III). (The actions of workers applying their mouthparts to the queen gaster, described above, have not been regarded as grooming in this context.) This increase in grooming of the queen could be related chiefly to the noticeable increase in soil on her body surface due to her high level of activity, or to accumulated refuse in her infrabuccal cavity, related to her high frequency of LHF. *Leptanilla* queens have not been observed to discharge infrabuccal pellets onto the substrate following each bout of LHF, as is ordinarily seen in *Amblyopone*, whose queens discharge one or two white filtered dregs of hemolymph from the infrabuccal cavity onto the floor of the nest after each bout of LHF (MASUKO, 1986).

Insect self-grooming behavior involves complex but stereotyped movements. This stereotypy permits systematic classification of movement patterns. Formicoid grooming repertoires have been summarized by WILSON (1962) and FARISH (1972). However, nothing has been known on these matters for the Leptanillinae. The characteristic movements used by *L. japonica* are described below, mainly with reference to the formulae provided by FARISH (1972).

(a) *Antennal grooming*: *Leptanilla* is unusual, in that the funiculi and scapes are separately groomed using different movements of the forelegs (L1). (i) *L1-funiculus grooming*: The antennal cleaner (the strigils of the tibial spur) of L1 is moved swiftly distad along the funiculi. Two methods were observed: 1) use of ipsilateral L1; 2) use of both L1, simultaneously on the same antenna. In the first method the funiculi of the same side are usually groomed 2 or more times in succession before transfer to the other side. This simple grooming is combined with other unit movements to form a composite of grooming movements, though it also frequently appears in isolation, in the course of other activities such as walking. (ii) *L1-scape grooming*: The scape of one antenna is quickly wiped with the ipsilateral L1. This movement occurs ordinarily in combination with both of L1-mouthparts grooming and head grooming.

(b) *L1-mouthparts grooming*: While the mandibles are open, the tarsi and distal parts of the tibiae of L1 first quickly wiped forward the ipsilateral surface of the lower

mouthparts, and then immediately are drawn back in the space between the maxilla and the labium. In this process, detritus attached to the fore tarsus is transferred to the infrabuccal chamber, as described by WILSON (1962).

(c) *Head grooming*: The sides of the head and the outer surface of the mandibles, while open, are wiped by a forward stroke of the ipsilateral L1, followed immediately by L1-mouthparts grooming. Additionally, wiping of the antennal scapes is usually combined with this series, forming the most complex grooming movement in *L. japonica*.

(d) *Thorax grooming*: (i) *Dorsum by L1*: The frontal corners of the prothorax are quickly wiped by the tarsi of L1, which movement progressively changes to head grooming. (ii) *Pleuron by L1*: Both L1 are reflexed back in an awkward manner, being folded at the femoral-tibial joint, and groom the pleura of the thorax in a sawing motion. The dorsal parts of the coxae of middle (L2) and hind (L3) legs also appear to be groomed with this movement.

(e) *L3-abdomen grooming*: The sides and the venter of the abdomen are wiped by the tarsi of the ipsilateral L3, each side being groomed alternately. During this movement, the abdomen is somewhat bent towards the leg being used. Usually, this movement is performed concurrently with the other grooming which use L1, but it also occurs independently while walking.

(f) *L1-L1 grooming*: One L1 is passed through the antennal cleaner of the opposite L1 alternately, both legs being raised off the floor. This grooming is remarkably frequent in *L. japonica*, punctuating most sequences of other grooming movements.

(g) *L1-L1-L2 grooming*: Both L1 are lifted in the air and wipe the tarsus of a single L2, but usually the ipsilateral L1 hardly reaches the L2 because of postural difficulty.

(h) *L1-L1-L2-L3 grooming*: This is essentially the same as L1-L1-L2 grooming, except that L3 on the same side as L2 is also incorporated.

(i) *L3-L3 grooming*: This involves the reciprocal movement of one L3 stroking the other beneath the abdomen, which is raised slightly.

The movements *a/i/i*, and *g/h/i* were recorded only from workers, and not from the queen. This may be due to the short observation period and does not necessarily indicate their absence from the queen's repertoire.

DISCUSSION

Although many details of the biology of *L. japonica* are far from verified, the dorsoventrally flattened body form of both adults and larvae, and the predation on soil-inhabiting centipedes, indicate that this ant is highly adapted for a totally subterranean life, involving movement through narrow preformed crevices. Its small colony size contrasts notably with that of the army ants. Colonies of dorylines and ecitonines are huge, and capture a broad spectrum of terrestrial arthropods, often including other social insects (GOTWALD, 1982). A physogastric queen of *L. japonica* lays a batch of 100-200 eggs within a few days. The estimated numbers of eggs delivered within the same period by *Eciton hamatum* and *E. burchelli* queens amount to 50,000 - 200,000 (RETTEMEYER, 1963; FRANKS, 1985). The total number of observed

ovarioles of an *L. japonica* queen was only 31-32, while a queen of *E. burchelli* may have a total of about 2,600 ovarioles (HAGAN, 1954). In *E. hamatum* the queen, which is about 20 mm long when contracted (SCHNEIRLA and BROWN, 1952), lays eggs of 0.3 mm diameter (SCHNEIRLA, 1971; his figure 8.8). Eggs of almost the same size (0.26 mm in the length) are produced by the much smaller *L. japonica* queen, which is only 1.8 mm long when contracted. Since the egg/queen size ratios are 0.015 in *E. hamatum* and 0.14 in *L. japonica*, the relative egg weight is probably approximately a thousand times greater in the latter. *E. hamatum* queens, however, produce about a thousand times as many eggs as *L. japonica*, so that egg production is fairly comparable in relative scale. Stated another way, army ant egg production is characterized by egg dwarfism, which is also evident in social bees and wasps (IWATA and SAKAGAMI, 1966). The multiplication of ovarioles is also widely observed in social Hymenoptera, especially in ant queens (IWATA and SAKAGAMI, 1966). Indubitably, these traits have evolved in relation to increase in the queen's fecundity, and, among ants, both are embodied in the reproduction of army ants.

Although details of predatory behavior of *L. japonica* remain unknown, the present study suggests that this ant is a specialist predator of geophilomorph centipedes and forage using a trail system. Considering the small body size and nest population of workers, it is probable that the trails in nature are short, probably no more than one meter in length. In nature the prey would be encountered and captured on or around the trails along which it is retrieved to the nest site, or, conversely (or often concurrently) all colony members migrate to the place of prey capture, as observed in my laboratory studies. In addition, the precocity of callow workers, impermanent use of nests, as suggested by field observations, the dichthadiiform queen with strong legs, and the larval structures forming a coupling mechanism for transportation, all indicate that *L. japonica* is a highly migratory ant. Considering the nature of the prey, however, daily nest relocation, as in army ant colonies during the nomadic phase, is improbable. Colony migration to a prey site, as observed in the laboratory, suggests that most migrations of *L. japonica* colonies occur at irregular intervals in response to successful prey capture, or as a result of prolonged food shortage, or some other environmental disturbance.

There is little information on sexual brood production and mating behavior in *L. japonica*. It seems probable that males move between nests in flight, seeking virgin females which do not leave their parent colonies to mate. If, as seems very probable, *L. japonica* is univoltine, coincidence between numbers of workers and mature larvae or pupae present in a colony would indicate that the adult life span of workers is normally one year, or a little more, and thus that yearly renewal of the total worker population occurs in colonies of this species. If this is the case, males and queens are

likely produced in normal broods along with workers, because entirely reproductive broods without workers, as reported for army ants (SCHNEIRLA and BROWN, 1952), would interrupt worker production for almost 2 years. Sexual dimorphism in *L. japonica* is greatly different from that known in army ants. Unlike the peculiarly large and robust males of army ants (FRANKS and HÖLDOBLER, 1987), the male of *L. japonica* is small and slightly-built compared to conspecific queens, as is general in the sexual dimorphism of ants (OGATA, TERAYAMA and MASUKO, in prep.). Lone males assigned by previous authors to the Leptanillinae have been caught in traps or by sweeping (PETERSEN, 1968; OGATA, pers. comm.), suggesting that the males leave the nests for mating. Judging from the apterous condition of the queens it is probable that new colonies are established by colony fission, as in army ants.

Larval hemolymph feeding by *Leptanilla* appears to be an adaptation to unstable food conditions affecting this specialist predator of relatively large prey, as in the apparent case in *Amblyopone silvestrii* (MASUKO, 1986, 1989). Both species lack the habit of regurgitation, so that, when food is depleted in a colony, the adults, especially the queens, can obtain nutrients only by cannibalizing brood. To feed on worker trophic eggs is also impossible for these ants. In *Amblyopone* the queen completely inhibits ovarian development in workers (probably through social dominance; MASUKO, 1987). In *Leptanilla*, the worker caste has no ovaries. Nondestructive use of brood as food, if it is possible, would be much more advantageous than cannibalism, and this could explain the evolution of LHF. Furthermore, for ants which produce broods cyclically, another plausible advantage is that LHF readily secures synchronization between larval maturation and oviposition by the queen (MASUKO, 1989). LHF or LHF-like feeding, utilizing mature larvae, possibly occurs also in army ants, however little is known about the nutrition of their queens (e.g. RETTENMEYER, 1963; SCHNEIRLA, 1971; GOTWALD, 1982). The larval hemolymph tap, which is unique to *Leptanilla*, may have evolved in order both to lessen the damage resulting from intensive LHF on a relatively small number of larvae, and to raise the efficiency of hemolymph transfer necessitated by the queen's rapid ovarian development, which is important in the strictly synchronous production of the brood (MASUKO, 1989).

L. japonica overwinters larvae. Production of new adults from posthibernating larvae is rather common both in ant species found in Manazuru forest (MASUKO, unpubl.) and in temperate species in general (ICHINOSE, 1987). In *L. japonica*, the brood event over a year is inevitable from the synchronization of pupation and oviposition. On the other hand, *Cerapachys humicola*, which is found in Manazuru forest and whose larvae develop and mature in synchrony, produces adults from eggs laid in the same year without overwintering (MASUKO, unpubl.). This brood production pattern may be

viewed as coincident with the observation that this species lacks the habit of LHF, which mediates pupation and oviposition in *L. japonica*.

In discussing the characteristics of army ant behavior WILSON (1958) took account only of colony migration ("nomadism") and group-predation. He did not emphasize cyclical brood production (or, more accurately, cyclical production of synchronously developing brood). In fact, the function of this phenomenon is rather obscure, although it is conceivable that the migration cycle has evolved to synchronize with the presence of the life stage requiring the greatest food supply (WILSON, 1971). When comparison is limited to tropical army ants, brood production is generally more cyclical in epigaecic species than in hypogaecic ones (GOTWALD, 1982). Apart from the army ants and *Leptanilla*, synchronous brood development is known in some other legionary or group-predatory ponerines such as *Onychomyrmex* (TAYLOR, cited in SCHNEIRLA, 1971, p. 167) and *Cerapachys* (HÖLDOBLER, 1982). On the other hand, the tropical dolichoderine ant *Dolichoderus cuspidatus*, which is truly "nomadic" (i.e. migrating with the symbiotic coccids with which it lives), produces broods acyclically (MASCHWITZ and HANEL, 1985). Similar noncyclical brood production is exhibited also by a temperate, queenless migratory myrmicine, *Pristomyrmex pungens* (TSUJI, pers. comm.). Since both species largely or exclusively depend on homopteran honeydew as nutrient, the nature of the food could be important in determining the brood production patterns of migratory ants. Yet brood production is acyclical in the tropical, carnivorous legionary ponerine *Leptogenys* sp. 1 near *mutabilis* (MASCHWITZ, STEGHAUS-KOVAC, GAUBE and HANEL, in prep.). Much more information is needed to illuminate the evolution and function(s) of cyclical brood production in migratory ants.

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References

- BARONI URBANI C., 1977. — Materiali per una revisione della sottofamiglia Leptanillinae Emery (Hymenoptera: Formicidae). *Entomol. Basil.*, 2, 427-488.
 EMERY C., 1910. — Hymenoptera. Fam. Formicidae Subfam. Dorylinae. In: P. Wytsman (ed.), *Genera Insectorum*, Fasc. 102, V. Verteneuill and L. Desmet, Brussels, 34 pp.

- FARISH D.J., 1972. — The evolutionary implications of qualitative variation in the grooming behaviour of the Hymenoptera (Insecta). *Anim. Behav.*, 20, 662-676.
- FRANKS N.R., 1985. — Reproduction, foraging efficiency and worker polymorphism in army ants. In: B. Hölldobler, M. Lindauer (eds.), *Experimental Behavioral Ecology*, G. Fischer Verlag, Stuttgart, pp. 90-107.
- FRANKS N.R., HÖLDOBLER B., 1987. — Sexual competition during colony reproduction in army ants. *Biol. J. Linn. Soc.*, 30, 229-245.
- GOTWALD W.H. Jr., 1982. — Army ants. In: H.R. Hermann (ed.), *Social Insects* vol. IV. Academic Press, New York, pp. 157-254.
- HAGAN H.R., 1954. — The reproductive system of the army-ant queen, *Eciton* (*Eciton*). Part 3. The oocyte cycle. *Am. Mus. Nov.*, 1665, 1-20.
- HÖLDOBLER B., 1982. — Communication, raiding behavior and prey storage in *Cerapachys* (Hymenoptera: Formicidae). *Psyche*, 89, 3-23.
- HÖLDOBLER B., TAYLOR R.W., 1982. — A new sternal gland in ants and its function in chemical communication. *Naturwissenschaften*, 69, 90.
- HÖLDOBLER B., PALMER J.M., MASUKO K., BROWN W.L. Jr., 1989. — New exocrine glands in the legionary ant genus *Leptanilla* Emery (Hymenoptera: Formicidae: Leptanillinae). *Zoomorphology*. (In press).
- ICHINOSE K., 1987. — Annual life cycle of *Paratrechina flavipes* (Hymenoptera, Formicidae) in the Tomakomai Experimental Forest, southern Hokkaido. *Kontyû, Tokyo*, 55, 9-20.
- IWATA K., SAKAGAMI S.F., 1966. — Gigantism and dwarfism in bee eggs in relation to the mode of life, with notes on the number of ovarioles. *Japn. J. Ecol.*, 16, 4-16.
- LE MASNE, G. 1953. — Observations sur les relations entre le couvain et les adultes chez les fourmis. *Ann. Sci. Nat. Zool. (Sér. 11)*, 15, 1-56.
- MASCHWITZ U., HÄNEL H., 1985. — The migrating herdsman *Dolichoderus* (*Diablotus*) *cuspidatus*: an ant with a novel mode of life. *Behav. Ecol. Sociobiol.*, 17, 171-184.
- MASUKO K., 1986. — Larval hemolymph feeding: a nondestructive parental cannibalism in the primitive ant *Amblyopone silvestrii* (Wheeler) (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.*, 19, 249-255.
- MASUKO K., 1987. — Ecology and sociobiology of the primitive ant *Amblyopone silvestrii* (Hymenoptera: Formicidae). Thesis, Tokyo Metropolitan University, 200 pp.
- MASUKO K., 1989. — Larval hemolymph feeding in the ant *Leptanilla japonica* by use of a specialized duct organ, the "larval hemolymph tap" (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.*, 24, 127-132.
- NATION J.L., 1983. — A new method using hexamethyldisilazane for preparation of soft insect tissue for scanning electron microscopy. *Stain Tech.*, 58, 347-351.
- PETERSEN B., 1968. — Some novelties in presumed males of Leptanillinae (Hym., Formicidae). *Entomol. Meddel.*, 36, 577-598.
- REITENMEYER C.W., 1963. — Behavioral studies of army ants. *Univ. Kansas Sci. Bull.*, 44, 281-465.
- SCHNEIRLA T.C., 1971. — *Army Ants: A Study in Social Organization*. W.H. Freeman & Co., San Francisco, 349 pp.
- SCHNEIRLA T.C., BROWN R.Z., 1952. — Sexual broods and the reproduction of young queens in two species of army ants. *Zoologica (N.Y.)*, 37, 5-32.
- WHEELER G.C., WHEELER E.W., 1930. — Two new ants from Java. *Psyche*, 37, 193-201.
- WHEELER G.C., WHEELER J., 1965. — The ant larvae of the subfamily Leptanillinae (Hymenoptera, Formicidae). *Psyche*, 72, 24-34.
- WHEELER G.C., WHEELER J., 1976. — Ant larvae: review and synthesis. *Mem. Entomol. Soc. Wash.*, no. 7, 108 pp.
- WHEELER W.M., 1923. — *Social Life among the Insects*. Harcourt, Brace and Company, New York, 375 pp.
- WILSON E.O., 1958. — The beginnings of nomadic and group-predatory behavior in the ponerine ants. *Evolution*, 12, 24-36.
- WILSON E.O., 1962. — Behavior of *Daceton armigerum* (Latreille), with a classification of self-grooming movements in ants. *Bull. Mus. Comp. Zool.*, 127, 401-422.
- WILSON E.O., 1971. — *The Insect Societies*. The Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts, 548 pp.